THE SUBLITTORAL ECOLOGY OF WEST ISLAND, SOUTH AUSTRALIA

1. ENVIRONMENTAL FEATURES AND THE ALGAL ECOLOGY

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SUMMARY

An account is given of the sublittoral marine algal ecology of West Island, a small island lying at the western end of Encounter Bay, South Australia. Environmental factors and the algal zonation and associations to a depth of 28 m are described.

On rough shores three zones are evident but on the sheltered lee shore the uppermost zone is very restricted and the lowermost zone does not occur due to the limited water depth. The upper sublittoral zone is colonised by a short red-algal turf comprising species tolerant of turbulent water and strong light, with a sublittoral fringe of *Cystophora intermedia* present only in the roughest areas. The mid sublittoral zone is dominated by larger brown algae and the lower sublittoral by a mixed association of red algae growing under conditions of low light and slight surge.

Water movement and light are probably the two most important ecological factors in the sublittoral. Horizontally species' range is largely determined by water movement but vertically light is the more important; however, it is evident that the mid sublittoral zone of large brown algae occurs at greater depth under rougher conditions, and several other species follow this pattern. The depth range of most species can vary considerably depending on the interplay of light, water movement, aspect and probably other less conspicuous factors.

Estimates are given of the standing crop of algae within various associations.

INTRODUCTION

Although the intertidal ecology of the southern Australian coast is fairly well known (Bennett & Pope 1953, 1960; Womersley 1947, 1948, 1956a; Womersley & Edmonds 1952, 1958), the only study within this region of the subtidal algal ecology and distribution, based on collections made in situ, is that in the almost enclosed Port Phillip Bay, Victoria (Womersley 1966).

This contrasts with the situation in the northern hemisphere where pioneer studies in subtidal ecology were made by Gislen (1930) in a Swedish fjord, using helmet diving equipment, and by Feldmann (1937) in the Mediterranean. With the advent of SCUBA equipment, sublittoral surveys have been carried out on many coasts, including those of Europe (Forster 1961, Jorde 1966, Kain 1960, Kitching 1941, Söderström 1965), the Mediterranean (Crossett & Larkum 1966, Pérès 1967, Vacelet 1967), Asia (Petrov 1967, Vozzhinskaya 1965), North America (Edelstein et al. 1969, McLean 1962, Neushul 1965), New Zealand (Bergquist 1960a,b) and the Antarctic (Zaneveld 1966).

Thus knowledge of subtidal marine organisms and their ecology in Australia is largely limited to the uppermost sublittoral as observed during very low tides or by shallow diving and visual observation from the surface. The sublittoral on rough coasts, which comprise most of the southern Australian coastline, is virtually unknown, though the rich algal flora has been fairly well documented from drift collections.

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The ecology of subtidal communities of marine algae and sea-grasses is of basic importance in many marine studies and, together with floristic studies of such communities, is a valuable indicator of the biogeographic relationships of a region. Subtidal, rather than intertidal, organisms are probably better for this purpose since they are not subject to the extremes of temperature and other conditions in the intertidal region.

West Island was chosen for study because of its easy accessibility yet suitable position subject to rough conditions with no protection from the south-west. Biotic communities on such off-shore islands generally have a richer flora and fauna than communities in more sheltered waters. This is probably because physical conditions in the water are more favourable and less variable. While water movement is usually greater around off-shore islands, fluctuations in temperature, salinity, oxygenation and turbidity are smaller and sand scour is almost absent. West Island is of a suitable size for a study of the effect of wave action which varies greatly from windward to lee shores around the island; also the presence of steep under-water slopes permits a study of communities in relation to depth.

The aspect of subtidal rock surfaces is of considerable importance. Upward facing surfaces are dominated by algae but, as a rock face approaches the vertical, faunal elements increase and algal density decreases. In caves, crevices and under overhangs, algae are mostly absent and animals predominate, as has been described by Crossett & Larkum (1966), Pérès & Picard (1949) and Vacelet (1967). This is due almost entirely to low light intensity and re-emphasizes that algae usually dominate the photic zone while animals dominate places where light is inadequate for plant growth. While some animal communities do occur within the photic zone, division of synecological studies into faunistic and floristic aspects is convenient. In the following account, horizontal and sloping to vertical surfaces are considered, but not other surfaces subject to reduced light where the fauna predominates. The animals which are prominent among the algal communities are mentioned briefly.

This account of the subtidal algal vegetation of West Island is of more than local interest, since many of the communities and the basic zonation are found elsewhere in rough areas of the central coast of South Australia. The intertidal zone is excluded from this account since the discussion of Womersley and Edmonds (1958) for rough to sheltered, steeply sloping coasts applies to West Island.

METHODS

The survey on which this study is based was carried out by the first author with SCUBA equipment between December 1965 and May 1968, with occasional observations since then. The island was visited on fifty occasions at fortnightly or monthly intervals during the study period and more than seventy hours were spent underwater. Notes were taken on sand-blasted perspex and algal (and faunal) collections were made at numerous localities about the island. Determinations of algae were made by the second author. Specimens of all species are lodged in the herbarium of the Botany Department, University of Adelaide (ADU).

All depths given in this paper are in metres and are based on the low water neap tide level for Victor Harbor. This "datum level" is used for Figures 7-14 and the eulittoral—sublittoral boundary varies from this as indicated on Figure 6.

Initially, a general survey was made of the area and the algae collected for identification. Then followed a more careful survey and the relative abundance and range of individual species were noted. Finally, quantitative estimates were made of the density of algae at several points about the island.

The continuous south-west swell made collecting difficult and hazardous on the southern and western shores, and the upper sublittoral zone at these localities was only accessible after days of protracted calm weather. On only two occasions during the period was the swell low enough to permit diving at upper levels at Lands End.

AREA SURVEYED

West Island (Pl. 1) is a granite knoll of about 13 hectares (33 acres) rising to a height of 40 m, about 800 m offshore at the north west end of Encounter Bay (Lat. 35°37′, Long. 138°35′). The island is figured and its geology discussed by Howchin (1910, p. 7, pl. XI). Some prominent features on the island and locality names used during the survey are shown in Figure 1 and Plate 1. Along the windward southern face, steep cliffs fall abruptly to the intertidal and continue to a sandy sea floor at a depth of about 29 m. Underwater the granitic blocks have broad sloping faces and form between them crevices, caverns and overhangs.

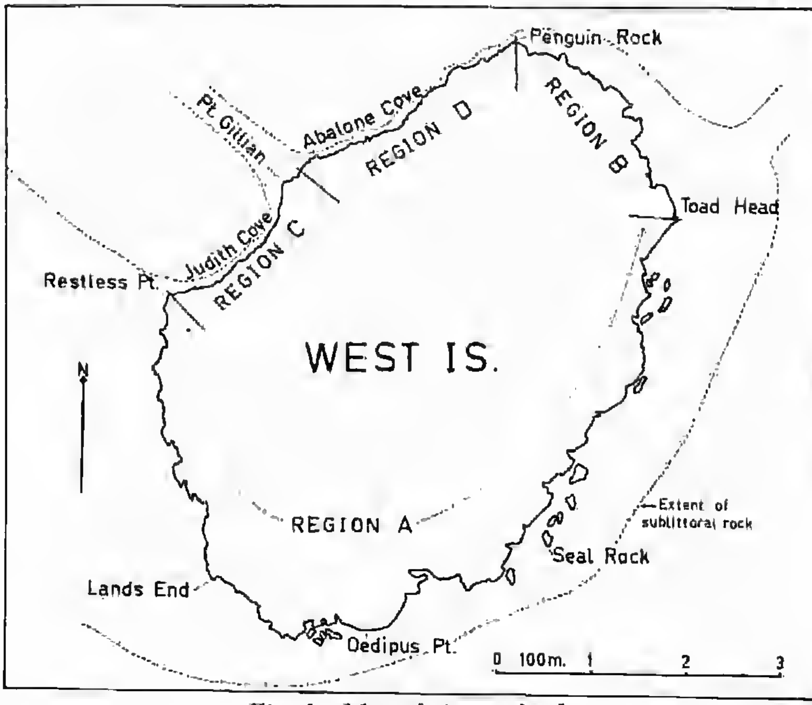


Fig. 1 Map of West Island.

While the underwater topography provides many different microhabitats with a great diversity of plants and animals, there are also extensive areas of uniform algal growth. Along the eastern and western shores the sea floor gradually rises (see Figure 4). The continual breakers on much of the western shore prevented a detailed examination of the sea floor. The northern shore of the island between Restless Point and Penguin Rock is low and slopes to the sea bed at about 5 m. In many places rounded granite boulders up to 50 cm across lie down the slope and are scattered on the bottom, and two shallow rocky sills run shorewards at a depth of about 3 m. To the lee of the island, extensive beds of marine angiosperms stabilize the sandy sea-bed.

ENVIRONMENTAL FACTORS

(a) *Temperature*

West Island is reported to lie between the summer and winter surface sea isotherms of 19° and 13°C (Womersley and Edmonds 1958). Temperature readings were taken from the surface to the bottom at 5 m intervals in the open sea outside the island, at monthly intervals for three years. Figure 2 shows that the annual range in surface temperature is about 8°C. Surface temperature readings from the winter of 1967 until the winter of 1968 were relatively high, averaging about 2°C above those recorded in the previous two years, while summer temperatures in 1969 and 1970 were lower, the highest readings being 19·5°C.

Temperatures did not vary greatly from the surface to the bottom. A thermocline was sometimes recorded between 15 and 20 m during calm periods in summer when the surface water was from 1-3°C warmer than deeper water. This was no doubt due to the heating by radiation of the upper water column, together with lack of mixing. Conversely, in late autumn, the surface waters cooled more quickly and were sometimes up to 1°C cooler than the water between 20 and 28 m. Between July and October a bottom layer of turbid water up to 3 m thick was sometimes found to vary up to 1°C above or below that of the superjacent water.

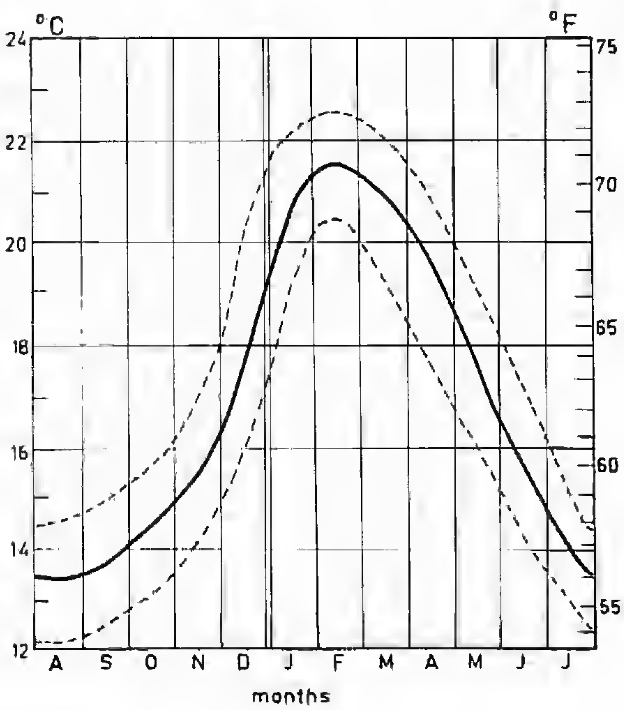


Fig. 2 Sea surface temperatures in 1965-67 taken 20-30 m off the south-east coast of West Island. The broken lines indicate the extreme range, and the solid line shows the averages for the period.

(b) *Waves, Swell and Surge*

Wave energy reaching the island is of three main types

(i) *Prevailing Swell.* This is generated in the Southern Ocean well south of the continent and prevails throughout the year; the direction of approach is south-west.

(ii) *Local Seas.* These are caused by local winds. When the winds are offshore (i.e. from the east through north to west) waves of short wave length (period < 3 seconds) are generated. These produce no surge and are of little significance in the sublittoral zone. On-shore winds produce waves which combine with the swell and reinforce it.

(iii) *Local Swell.* In early summer (November and December), the prevailing winds are from the south to south-east. During these months a short swell is generated from that direction with a period of 5 to 6 seconds. This may be superimposed on the prevailing swell causing the combined swells to periodically reinforce each other. Local swell is unusual at other times of the year.

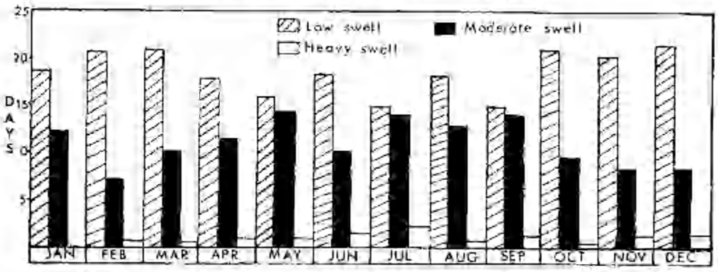


Fig. 3 Average monthly distribution of days of low, moderate and heavy swell for the years 1965-1967 at Neptune Is.

Prevailing swell conditions from 1965 to 1967 as recorded at Neptune Island (at the southern end of Spencer Gulf) are shown in Figure 3 and indicate the situation at West Island. Although oceanic swell is on the average more severe during winter, periods of very low swell may occur at any time of the year.

The observed swell characteristics are shown in Table 1. Wave lengths were determined from aerial photographs.

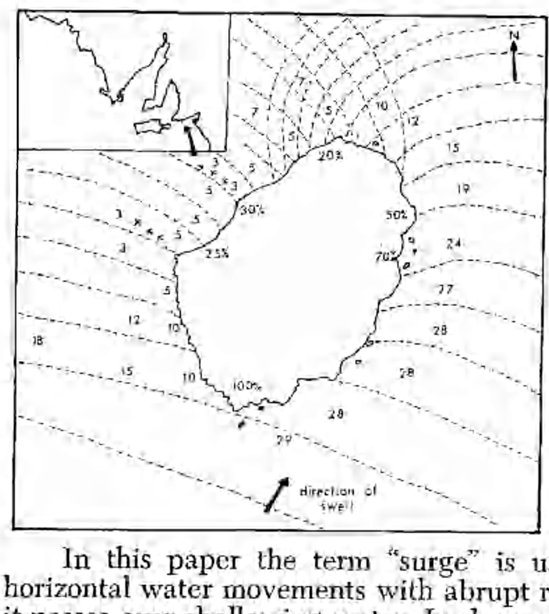


Fig. 4 Successive wave crests (broken lines) about West Island. Figures (within the island outline) are wave heights expressed as percentage of maximum height at Lands End. Depths are in metres. The position of West Island is shown on the inset map of the South Australian coast.

In this paper the term "surge" is used to refer to the rapid sub-surface horizontal water movements with abrupt reversals of flow caused by the swell as it passes over shallowing water. In deep water, as a wave passes, any particle of water describes a circle the radius of which decreases with depth. However, on approaching an island barrier the water will surge to and fro more or less horizontally. This effect is most severe near the surface and decreases with depth.

TABLE 1

Observed prevailing swell conditions at West Island

Swell	Wave Height Range (metres)	Period (seconds)	Wave Length (metres)
Low	(0·5—) 1—2	10 — 12	110 — 120
Moderate	2 — 3		
Heavy	over 3		

The degree of water movement is of great significance in its effect upon algal growth but it has not yet been satisfactorily measured. The methods of Jones and Demetropoulos (1965, 1968) and Muus (1968) are not readily applicable to under-water studies. Despite the lack of accurate measurements, biological indicators and some local knowledge will generally enable a reasonably good assessment of surge conditions to be made. There is no doubt that occasional very rough seas do more damage to algae by mechanical action of surge than do average conditions.

The prevailing swell strikes the island on the southern and western shores, reaching maximal force at Lands End. The distribution of wave height about the island is controlled largely by diffractive effects although on the northern shore some wave refraction occurs inshore (see Figure 4). The two submerged reefs on the northern shore and the dense sea-grass meadows in shallow water cumulatively attenuate the swell so that in Abalone Cove it is reduced to about 20% of its original height. At Abalone Cove the waves passing around each side of the island intersect, resulting in a continual though slight surge. Figure 4 shows successive wave crests and estimated wave heights at various localities expressed as a percentage of wave height at the roughest location.

(c) *Visibility and Submarine Illumination*

The island is washed by oceanic water which is virtually free from suspended silt discharged from mainland rivers. Occasionally (usually September to November) after strong southerlies, tongues of turbid water may extend westward from the River Murray mouth (about 24 km to the east) to the vicinity of West Island, but these are rapidly dispersed by a change in weather.

TABLE 2

Underwater Visibility off West Island

Conditions	Visibility at depth of 0 — 20m	20 — 29m
1. *October to February*		
Low Swell	7 — 12m	2 — 5m
Moderate Swell	About 5m	1 — 2m
2. *March to September*		
Low Swell	10 — 15m	3 — 10m
Moderate Swell	5 — 7m	1 — 2m

Visibility is fairly uniform down to about 20 m but below this drops sharply. The degree of turbidity is related to swell conditions. Bottom sediments are stirred up through agitation of the sea-bed by surge and water turbidity is greatest near the bottom, depending on the duration and severity of the swell. The approximate range of visibility during the year is shown in Table 2. After a prolonged calm, visibility near the bottom may rise to the maximum shown in the Table but usually lies between 1 and 4 m.

Water transparency was found to be generally lower during summer than at other times. An increase in plankton may be responsible for the reduction in transparency, but this has not been investigated.

Light readings using a photometer in a watertight case were taken from the surface to the bottom at 5 m intervals outside the island, monthly for 12 months. The readings were all taken with the sun at zenith and with a clear sky. Light intensities vary according to water turbidity and the range in values down to 26 m (expressed as a percentage of subsurface illumination) is shown in Figure 5. The illumination for clearest and average oceanic water and for average coastal water (after Sverdrup et al. 1942, p. 776) is also given in Figure 5 for comparison. The transmission values for the waters off West Island lie between the values for average ocean water and average coastal water.

In addition the horizontal illumination was measured at various depths to determine the intensity of light falling on a vertical rock face (Poole and Atkins 1929, Strickland 1958, p. 472). The ratio of horizontal to downward illumination at various depths is shown in Table 3. The highest percentages were recorded from waters of average transparency and the lowest from turbid water; the percentages for very clear water were slightly below the averages recorded. On rare occasions, however, near the bottom, light reflected upward from the sand increased the level of light by as much as 50%.

TABLE 3

Ratios of horizontal to downward illumination at various depths expressed as a percentage of downward illumination

Depth (metres)	Subsurface	6	13	19	26
Extreme Range (%)	20 — 25	25 — 75	10 — 50	10 — 40	10 — 25
Average %	24	38	33	21	17

(d) *Scour and Sedimentation*

Scour by sand does not occur due to the absence of surge at the sublittoral base of the island where rock meets the sand. The waters of these rough shores are free from sediment, so that silt is absent from rock surfaces to at least 25 m. Below this depth sediments stirred up by swell may sometimes settle on rock. On the lee of the island also, sediments of fine sand may accumulate on a horizontal rock surface which is in an exceptionally protected site.

(e) *Other Factors*

No measurements were made of salinity, phosphate, nitrate, alkalinity or of the level of dissolved oxygen. The figures given by Womersley (1947, p. 235) for the south coast of Kangaroo Island are probably applicable to West Island. Kirkwood (1967) gives figures for organic phosphorus, inorganic phosphate and nitrate in South Australian waters. These factors are so stable that they are unlikely to contribute to community differences in the region studied.

TERMINOLOGY

With the probable development of further underwater studies, there is a need for uniformity in terminology. The proposals made here are applicable to southern Australian coasts and accord with observations made elsewhere by many other authors.

(1) *Horizontal Distribution*

On rough coasts of southern Australia surge is a principal factor affecting algal distribution (Womersley 1947, p. 236) and hence a classification of the benthic-plant environment should be related to this factor. The coastal sub-formations of Womersley (1947) might be adapted for sublittoral conditions as follows:

Rough coast sub-formation (i.e. subject to prevailing swell).

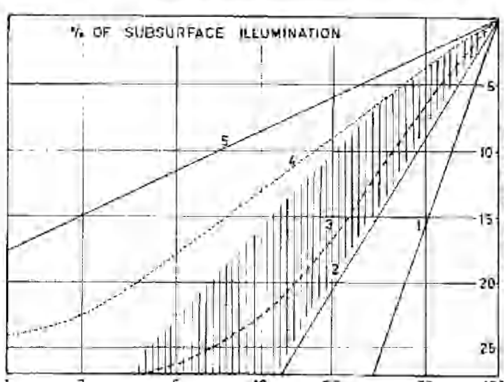
(i) Strong to extreme surge.

(ii) Moderate surge.

Womersley's "sheltered rocky coast sub-formation" then refers to a coast subject to a slight surge caused by swell or by wind-driven waves of short wave length. Bennett and Pope (1960, p. 221) use similar degrees of roughness and take the wave strength at Cape Bridgewater as a standard maximum. Wave action at Lands End, although not as severe as that at Cape Bridgewater, is of the same order.

(2) *Vertical Zonation*

A sharp distinction between zones is less apparent in the sublittoral than in the intertidal zone and plant zonation is seen rather as a gradation from one association to another. Nevertheless Jorde and Klavestad (1963) and Neushul (1965) describe three vertical algal zones and Bergquist (1960a,b), McLean (1962), Jorde (1966), Petrov (1967) and others describe an upper and lower zone in the sublittoral. In southern Australia usually three, sometimes two, zones according to locality and roughness, can be recognised. Figure 6 illustrates the terminology used. Most writers recognise similar vertical subdivisions (see Hedgpeth (1957, p. 19) and Petrov (1967) where the terminology used by various



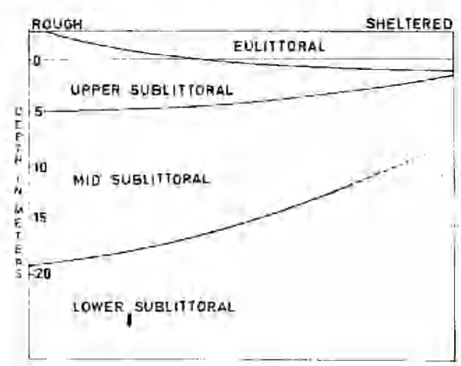


Fig. 5 (left) Range in transmission values for waters off West Island during low swell are shown in the shaded area. Other values are: 1. Clearest ocean water (after Sverdrup). 2. Average ocean water (after Sverdrup). 3. Average of values recorded during low swell. 4. Most turbid water recorded during moderate swell. 5. Average coastal water (after Sverdrup).

Fig. 6 (right) Zones of the sublittoral showing the depth variation from rough to sheltered water.

writers is summarised), the differences between them being in naming of the zones only. Pérès (1967) discusses a similar scheme based on intensity of water movement at different depths.

The term "upper sublittoral" refers to the upper zone which on most coasts is characterised by a short algal turf but on rough coasts in the cooler waters of Victoria and Tasmania is dominated by the "bull-kelp", *Durvillea potatorum*. On rough coasts the zone may descend to 5 m; in these conditions the highest part, emergent between waves at low tide, is characterised by distinctive species (e.g. *Cystophora intermedia*) and is referred to as the sublittoral fringe (Womersley and Edmonds 1952; Bennett and Pope 1960, p. 198).

The mid and lower levels of the sublittoral are characterised by communities of brown algae and red algae respectively.

These zones are biologically characterised entities and their boundaries vary according to the physical conditions. Figure 6 shows the shift in boundaries from rough to sheltered conditions. The most striking effect is that under sheltered conditions the upper sublittoral zone of algal turf is very narrow and the mid sublittoral zone of brown algae extends to low tide level.

(3) *Association and community*

The term "association" is used as in intertidal ecology (e.g. Womersley 1948) to refer to distinctive groupings of one or more species occurring repeatedly in a particular environment. The term "community" is less precise and refers generally to moderately distinct aggregations of plants. Further characterisation of ecological groupings in the sub-littoral must depend on future studies and at this stage more precise definitions are not attempted.

ZONATION AND DISTRIBUTION AROUND THE ISLAND

The general features of the algal vegetation change markedly around the island in passing from rough to more sheltered coasts. The shores have therefore been divided into four regions, each of which has algal communities with characteristic features. The changes in the vegetation from one region to another are seldom sharp yet occur over a relatively short distance, indicating a distinct gradient in one or more environmental factors.

(I) *Region A*. The rough-water southern and western coasts between Toad Head and Restless Point.

(II) *Regions B and C*. The moderately rough-water disjunct sections on the eastern and northern shores.

(III) *Region D*. The semi-sheltered section in Abalone Cove.

(1). *REGION A (ROUGH WATER)*

Wave action is generally strong and reaches its greatest force on the south-western side. Here the splash zone extends upwards to more than 20 m above sea level and the littorinid snail *Melaraphe unifasciata* (Gray) is common at this height. In conditions of such extreme roughness, both the eulittoral zone and the upper boundary of the sublittoral zone are elevated relative to mean sea level (cf. Söderström 1965), and *Cystophora intermedia* which has been used as an indicator of the upper boundary of the sublittoral (Womersley and Edmonds 1958) forms a narrow belt (sublittoral fringe) up to a metre wide. A vegetation profile down to 27 m in an area of extreme roughness at Lands End is given in Figure 7.

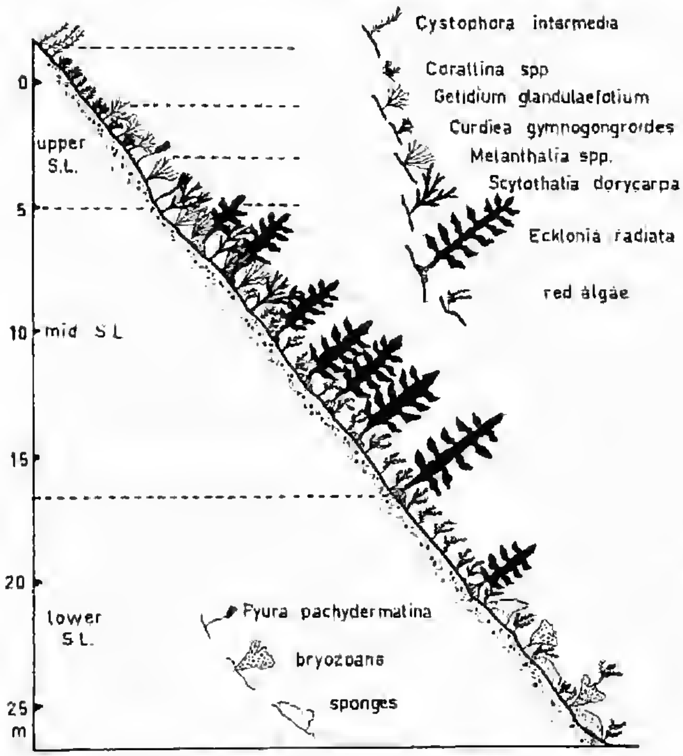


Fig. 7. A vegetation profile near Lands End (very rough). Three belts in the upper sublittoral are indicated by broken lines on the right of this zone.

Upper Sublittoral Zone (to 3-5 m deep)

A strong surge exists down to at least 12 m and it is seldom possible to examine underwater the region just below low water level. The zone is clearly defined and extends vertically down to between 3 and 5 m according to the degree of water turbulence. Along the western shore, on sloping faces, the zone contains three distinct horizontal belts.

(1) The uppermost is colonized by *Corallina* sp. and encrusting lithothamnia down to 1 m. *Pterocladia capillacea* occurs where there is local shelter near Restless Point. The corallines form a community with the barnacle *Balanus nigrescens* (Lamarck) and the chiton *Poneroplax costata* (Blainville). Occasionally, the mollusc *Dicathais textiliosa* (Lamarck) is also seen. The upper limit of the belt is indicated by *Cystophora intermedia* which, on horizontal rocks, forms a dense community but on sloping rocks occurs only in scattered clumps. This community also extends above *Cystophora intermedia* to form the lower eulittoral zone (see Womersley and Edmonds 1958) and it is now apparent that on such rough coasts there is a fairly uniform coralline mat—*Balanus* association extending for some distance above and below the low tide region (through and beyond the 'suck back' region) with a superimposed belt of *Cystophora intermedia* occurring where it is subject to momentary emergence at low tide.

(2) Below the corallines, there is a well defined middle belt comprising a mat chiefly of *Gelidium glandulaefolium* and *Curdiea gymnogongroides*. This mat extends to the lowest part of the zone but in its lowest 2 m tends to be overshadowed by more prominent species of the belt below.

(3) The lowest belt is characterised by larger algae, including *Melanthalia concinna*, *M. obtusata*, *Sargassum bracteolosum*, *Zonaria sinclairii* and occasionally *Scytothalia dorycarpa*, and forms a transition zone to the mid sublittoral zone dominated by *Ecklonia radiata*. The stalked ascidian, *Pyura pachydermatina* (Herdman) var. *gibbosa* Herdman is common below about 2 m.

Where the rock face drops vertically into the sublittoral and on much of the steep and shaded southern shore, three distinct belts are not evident. Probably due to the lower light intensity, corallines are scarce and the upper sublittoral is dominated by *Gelidium glandulaefolium*, *Curdiea gymnogongroides* and *Zonaria sinclairii*. Lower down in the zone, particularly on steep faces, *Plocamium angustum*, *Rhodymenia australis* and *Pterocladia lucida* may occur in addition to the prominent species of this level referred to previously.

Mid Sublittoral Zone (5-15 (-19) m deep)

The upper boundary of the zone is sharply defined by the appearance of the laminarian *Ecklonia radiata* which dominates the zone and extends even into the lower sublittoral. *Ecklonia* is co-dominant with *Melanthalia* spp. and other brown algae at upper levels of the mid sublittoral where they form a dense canopy. (See *Ecklonia-Melanthalia* Community where the species are listed). Where agitation of the water is most severe, the undergrowth is sparse and in many places the rock is covered with a crust of lithothamnia.

Below about 10 m some minor changes in the vegetation occur. Brown algae (except *Ecklonia*) become sparse and a red algal undergrowth occurs under the canopy of *Ecklonia*. Toward the lower limit of the zone, *Ecklonia* becomes scattered and the red algal element increases.

There are no noticeable qualitative differences between the vegetation on vertical and on horizontal surfaces where the surge is active, i.e. to about 10 m depth on the rough shore (A), decreasing to about 1 m in the sheltered parts of Region B. However upper-storey species (mainly brown algae) are less prominent while under-storey species are more conspicuous on vertical than on level surfaces. With increasing depth (over 10 m) brown algae disappear rapidly from vertical faces and a red algal community is established, usually epizoic on a ground community of calcareous bryozoans (mainly Reteporidae). Some algae appear restricted to or have a strong preference for vertical faces. These are *Cheilosporum elegans*, *Epiphloea bullosa*, *Thamnoclonium dichotomum*, *Laurencia clavata*, *L. elata* and *L. filiformis*.

Lower Sublittoral Zone (17-29 m deep)

The occurrence of a uniform red algal community in this zone is discussed in detail later. Red algae form a dense cover on upward facing rocks but on steep slopes are sparse (Figure 11). Here the tough and wiry algae of shallow water are replaced by delicate, filamentous or flabellate species. Near the base of the island at 25-28 m, algae are sparse and the rock face is covered by sessile fauna. Large sponges, the ascidians *Herdmania momus* (Savigny) var. *grandis* Heller and *Styela etheridgii* Herdman are prominent. Bryozoan colonies of *Retepora* spp. and *Adeona grisea* Lamouroux are abundant in places and provide a substrate for some algae e.g. *Thamnoclonium dichotomum* and *Plocamium* spp. Less prominent but quite common are stands of the hydroids *Plumularia procumbens* Spencer, *Sertularella lata* Bale and occasionally *Thecocarpus divaricatus* Bale; orange and white gorgonians, crinoids and crustacea are abundant.

(II). *REGIONS B AND C (MODERATELY ROUGH WATER)*

These are regions of constant surge but lack the extremely rough conditions of the southern and western shores. Toad Head and Restless Point are the natural outer boundaries of the two regions as they mark the transition in the mid sublittoral from communities of few species dominated by *Ecklonia* to those in which there is a more varied brown algal vegetation. *Cystophora intermedia* disappears from the sublittoral fringe at about these points and is generally absent in regions B and C. Communities of green algae are common in more sheltered parts.

At the inner boundaries respectively (Point Gillian and Penguin Rock) the wealth of algae decreases markedly. Due to the shallower depths in the two regions a lower sublittoral zone is generally absent.

Upper Sublittoral Zone

From Toad Head northwards towards Penguin Rock the upper sublittoral decreases from 3 m broad to less than 1 m; it is occupied by a short and dense algal turf with often a thin encrusing sponge as a basal matrix. *Ulva lactuca* is often common at the upper limit of the zone. In the rougher parts of the regions, the algal turf comprises a *Corallina-Zonaria* community towards its lower limit, or further up on vertical faces the following species are frequently seen: *Halopteris funicularis, H. gracilescens, Lobospira bicuspidata, Areschougia laurencia, Ballia callitricha* (stunted).

The lower limit of the zone is often not clearly defined and some species more characteristic of the mid sublittoral may occur, e.g. *Cystophora moniliformis, C. subfarcinata, Scytothalia dorycarpa, Seirococcus axillaris, Sargassum verruculosum, Plocamium costatum.*

In more sheltered parts of the regions, the zone bears a *Pterocladia capillacea* association descending for about 1 m until it merges with the vegetation of the mid sublittoral zone. However, an *Amphiroa-Corallina* association is able to displace the mat of *Pterocladia* in a sunny aspect and in well-agitated water; in places, it dominates the slope from low water level to about 4 m deep.

Three communities of green algae are often seen. Between 1 and 2 m depth *Caulerpa brownii* occurs either as a monospecific community on horizontal rock surfaces or among the *Amphiroa-Corallina* community at the same depth. A little deeper between 2 and 4 m a *Caulerpa flexilis* community is common on horizontal rock faces. Occasionally a *Caulerpa obscura* community occurs at about 3 to 4 m.

Mid Sublittoral Zone

In the upper part of the zone, a fucoid association forms a dense cover over the rocks. The preference of algae for upward facing rocks with increasing depth has been described and is evident in this zone. The vegetation near the sublittoral base of the island is poor and limited to a few species of which the brown alga *Glossophora nigricans* is prominent. The poverty of algal growth is probably due to the presence of fine sediments on the rocks as is indicated by the common occurrence of the bulky ascidians *Herdmania momus* var. *grandis* and *Ascidia sydneyensis* Stimpson.

(III). *REGION D (ABALONE COVE)*

The depth of water is limited to 5 m and there is a general decrease in the number of species compared to other regions; the lower sublittoral zone is not present.

Upper Sublittoral Zone

This is very narrow (0-0·5 m) and is represented only by a dense mat of *Pterocladia capillacea*. At the boundaries of region D, where wave-action increases slightly, corallines are more in evidence and tend to displace the *Pterocladia* mat.

Mid Sublittoral Zone

Part of this area has a solid granite substrate and the remainder has a loose boulder slope with rounded stones up to 50 cm across. The vegetation varies according to the type of bottom. Small stones are unstable and do not support large brown algae. The solid rock bears a "forest" of *Ecklonia* (up to 80 cm high) with very few undergrowth species except for a thin crust of lithothamnia. Steep or vertical slopes, however, have small numbers of the following species: *Halopteris funicularis*, *H. gracilescens*, *H. pseudospicata*, *Dictyota diemensis*, *Zonaria angustata*, *Z. crenata*, *Z. spiralis*, *Sargassum verruculosum*, *Cheilosporum elegans*. These species are also common on all except the smallest stones of the boulder slope. The bright orange jointed bryozoan *Catenicella margaritacea* Busk is also conspicuous in this zone.

At about 3 m depth *Ecklonia* is largely replaced by species common in the fucoid association, namely—*Acrocarpia paniculata*, *Cystophora monilifera*, *C. moniliformis*, *C. subfarcinata* and the coralline algae *Cheilosporum elegans* and *Metagoniolithon charoides*. Nearby, the sandy bottom supports dense beds of the marine angiosperms *Amphibolis antarctica*, *A. griffithii*, *Posidonia australis* (narrow leaf form) and *Heterozostera tasmanica*. These sea-grass communities have not been studied in detail.

(IV). *ALGAL ASSOCIATIONS AND COMMUNITIES*

The associations and communities recognised about the island are described below. Communities of the eulittoral zone were not specifically studied and are only discussed where they extend into the sublittoral.

A list of the commoner algae, from the four regions recognised and with known depth ranges, is given in the Appendix.

1. Coralline Association

Many corallines tolerate strong light and occur commonly in the lower eulittoral and upper sublittoral. At West Island corallines are not prominent on the steeply sloping and shaded southern and eastern shores but are common elsewhere.

(a) *Corallina community*

Corallina sp.

Conditions:—Moderate to strong turbulence.

Vertical Range:—Lower eulittoral down to 1 m.

The community is well developed along the western shore of Region A, especially on horizontal or gently sloping rocks. The association with the barnacle *Balanus nigrescens* and certain molluscs has already been described (p. 114). This community extends into the lower eulittoral where *Balanus* may become dominant in some localities (as also described for Point Sinclair, Eyre Pen. (Womersley and Edmonds 1958)). In very rough conditions the community appears as short tufted groups of plants scarcely 5 cm high, but in more sheltered places plants are denser and may show a vivid pink growth to about 7-8 cm in height.

(b) *Amphiroa-Corallina Community*

Common:—*Amphiroa anceps, Corallina cuvieri, Cheilosporum elegans.* Occasional:—*Corallina* sp.

Conditions:—Moderate turbulence.

Vertical Range: 0-5 m.

This community is prominent in Region C and portion of Region D near Penguin Rock and in optimal conditions forms a very dense turf to about 10 cm in height. Toward its lower limit, calcareous algal fragments accumulate among the living plants providing a haven for worms, crustaceans and molluscs. The proportions in which the component species occur may vary with depth as shown in Figure 13. Between 3 and 4 m, *Cheilosporum elegans* characteristically forms a pure stand on steep or vertical faces. Other species such as *Caulerpa brownii, Pterocladia lucida* and *Melanthalia obtusata* occasionally occur. This community is seen in similar habitats along much of the central Flindersian province of southern Australia.

(c) *Corallina-Zonaria Community*

Common:—*Zonaria sinclairii, Corallina cuvieri.* Fairly common:—*Sargassum bracteolosum, Cheilosporum elegans.* Occasional:—*Caulerpa brownii.*

Conditions:—Moderate turbulence.

Vertical Range: 0-3 m deep.

The community is well developed in moderately rough situations. It constitutes the uppermost sublittoral zone in Region B and also may be found in small stands in Region C. The development of *Sargassum bracteolosum* is seasonal: from February to September only the basal leaves are seen and the community is dominated by *Corallina cuvieri* and *Zonaria sinclairii* which forms a dense mat between 5 and 10 cm in height. In spring, *Sargassum bracteolosum* rapidly develops fertile fronds reaching 30 cm or more, then overshadowing the other components; these fertile fronds are completely lost again by February.

With increasing turbulence, *Corallina cuvieri* and *Sargassum bracteolosum* become sparse so that in some places there is an almost pure community of *Zonaria sinclairii.* This is seen mostly on gently sloping rock where the water is well agitated, and the community may continue into the lower eulittoral. The following species are more commonly seen on steep faces or toward the lower limit of the community—*Halopteris gracilescens, H. funicularis, Lobospira bicuspidata, Cheilosporum elegans, Areschougia dumosa.* It is uncertain whether their preference for a steep surface is due to a lower light requirement, a lower tolerance of surge, or both.

2. Pterocladia Capillacea Association

Common:—*Pterocladia capillacea.* Fairly common:—*Sargassum bracteolosum, Asparagopsis armata, Plocamium angustum.*

A number of other species occur but these are probably the outliers of communities lower down in the sublittoral. The following have been recorded at various times but are usually stunted in form and not common.

Caulerpa flexilis, C. obscura, Dictyota diemensis, Zonaria sinclairii, Z. spiralis, Cystophora subfarcinata, Corallina cuvieri, Melanthalia obtusata, Laurencia elata.

Conditions:—Slight to moderate surge, with a preference for steep or vertical faces. Where the surge is more severe the association is displaced by corallines.

Vertical range: 0-2 m.

In Region D the association forms a dense turf between 5 and 10 cm high, down to about 1 m depth where it gives way to the laminarian *Ecklonia*. In Judith Cove (Region C) it may extend down to about 2 m where it is replaced by various brown algae. At very low tide the upper part of the association is just emergent and in the summer the upper plants are often bleached by the sun. *Corallina* sp. occurs occasionally and *Asparagopsis armata* is often epiphytic on the *Pterocladia*. The community has only occasionally been noted elsewhere in South Australia in similar conditions.

3. Gelidium Glandulaefolium–Curdiea Gymnogongroides Association

Common:—*Gelidium glandulaefolium*, *Curdiea gymnogongroides*. Fairly common:—*Melanthalia concinna*, *M. obtusata*. Occasional:—*Zonaria sinclairii*, *Polyopes constrictus*.

Conditions—Extreme turbulence on steep faces.

Vertical Range:—from 1 to 3 m below low water.

This association is present at Lands End below the Coralline Association. It is most evident on steep or vertical rock faces, with the common species growing up to about 8 cm high. It forms a community with the barnacle *Balanus nigrescens* and the stalked ascidian *Pyura pachydermatina* var. *gibbosa*.

Occasionally, a mixed *Corallina-Gelidium* community is seen in places where the surge is strong but not severe. With increasing depth, the association becomes subordinate to the brown algae *Ecklonia* and *Scytothalia*.

4. Fucoid Association

Common:—*Acrocarpia paniculata*, *Cystophora monilifera*, *C. moniliformis*, *C. platylobium*, *C. subfarcinata*, *Seirococcus axillaris*, *Asparagopsis armata*. Fairly common:—*Scytothalia dorycarpa*. Occasional:—*Perithalia caudata*, *Ecklonia radiata*, *Sargassum bracteolosum*.

Conditions:—Moderate surge.

Vertical Range: 3-18 m deep (in calmer situations 1-10 m deep).

A dense vegetation of fucoid algae is a characteristic feature of rocky substrates on moderately rough shores of southern Australia; this community occurs throughout Regions B and C, and on some coasts in South Australia reaches to low tide level.

The structure of the association is complex; its vegetation is usually two-layered, but occasionally three-layered. The dense upper layer, ranging from 50 cm to 1 m in height, is dominated by fucoids, the individual species of which may occur in stands up to 10 m^2 in area, or sometimes as single or small groups of plants. The dissected and irregular nature of the rock surface on which the vegetation occurs creates numerous microhabitats with differing light and surge, resulting in a complex mosaic. Different species tend to be dominant at different depths. Figure 10 shows the vertical range of some species in Region B.

Ecklonia radiata is surprisingly sparse, being absent from most level surfaces but present on steep faces just below the lip of flat-topped rocks. In deeper water of 18 to 20 m, *Ecklonia* persists in a predominantly red algal community.

The middle layer is less complex; its height is from 10 to 20 cm and individual plants generally lie scattered and hidden under the shade of the prominent fucoid algae. At 5 m the undergrowth is mostly *Cheilosporum elegans*; at 8 m, *Zonaria* spp., *Corallina cuvieri*, *Halopteris* spp., *Plocamium angustum* and *Phacelocarpus labillardieri* occur. Between 10 m and 18 m the following species comprise the undergrowth: *Lobospira bicuspidata*, *Zonaria spiralis*, *Asparagopsis*

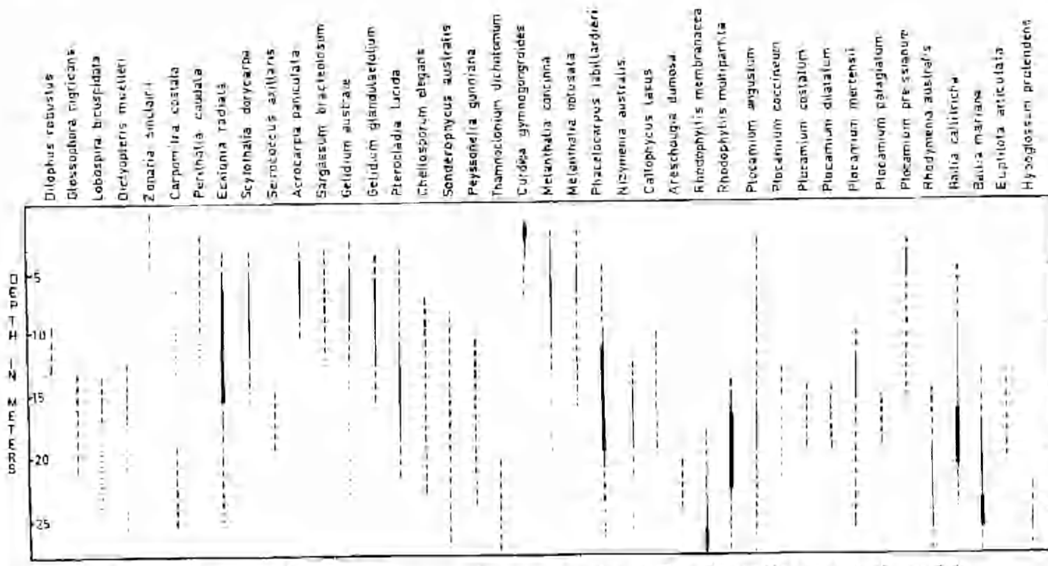


Fig. 8 Vertical range of some common algae on horizontal rock in Region A (rough). ——— common (shown by a thicker line where dominant); — — — — occasional; . . . . rare.

armata, *Peyssonelia gunniana*, *Phacelocarpus labillardieri*, *Plocamium angustum*, *P. mertensii*, *Rhodophyllis multipartita*, *Areschougia dumosa*, *Mychodia hamata* and *Osmundaria prolifera*.

At 18-20 m deep, the upper layer comprises mainly *Ecklonia* and *Cystophora platylobium* and is much less dense than in shallower water. On many slopes stands of *Plocamium* spp. are well developed. Here also a ground layer of prostrate species occurs, e.g. *Peyssonelia gunniana*, *P. novae-hollandiae* and *Sonderophycus australis*.

With increasing shelter there are minor changes in the association. Some species become more common, e.g. *Sargassum verruculosum*, *Corallina* sp., *Metagoniolithon charoides* and *Metamastophora flabellata*. Figure 15 shows the horizontal distribution of some of these species.

In Region C where similar surge conditions exist, the vegetation patterns typical of the upper part of the association in Region B are seen. The undergrowth species are mainly *Metamastophora flabellata*, *Metagoniolithon charoides*, *Cheilosporum elegans* and *Corallina* sp.

Floristically, the association is very rich and the total number of species collected is about 80.

5. Ecklonia Radiata Association

Ecklonia radiata is one of the most important and conspicuous zone-forming species of algae of southern Australia. It is prominent at West Island where it dominates two habitats on the rough and sheltered sides of the island respectively. In each habitat, *Ecklonia* constitutes the bulk of the vegetation (Figures 9, 14). In Region A, it characterises a community in water 3 to 18 m deep and in the sheltered Region D it occurs from about low water down to 5 m. Each community will be discussed in turn.

Why *Ecklonia* is not more common on the moderately rough shores of Region B is puzzling. It is possible that this laminarian may be unable to compete well with fucoid algae where conditions are optimal for their development.

Ecklonia—Melanthalia community

Common:—*Ecklonia radiata, Scytothalia dorycarpa, Melanthalia concinna.* Fairly common:—*Acrocarpia paniculata, Sargassum bracteolosum, Melanthalia obtusata.* Occasional:—*Seirococcus axillaris, Perithalia caudata.*

Undergrowth—Common:—*Gelidium glandulaefolium.* Fairly common:—*Pterocladia lucida, Phacelocarpus labillardieri, Plocamium preissianum.* Occasional:—*Zonaria sinclairii, Corallina* sp., *Polypes constrictus, Callophycus laxus, Ballia callitricha.*

Conditions:—Strong to extreme surge.

Vertical Range:—4-10 (-14) m deep.

The species listed are all able to stand extreme water movement. The structure of the community is two-layered. The upper layer consists of *Ecklonia, Scytothalia, Seirococcus* and *Acrocarpia.* Under these plants, an understorey of algae growing to about 20 cm in height occurs. The turbulence is too great for most animals except *Pyura pachydermatina* var. *gibbosa* and compound ascidians which colonise steep faces. The vertical ranges of the algae are shown in Figure 8.

Ecklonia community

Ecklonia radiata and encrusting lithothamnia.

Conditions:—Slight continuous surge.

Vertical Range:—0-4 m deep.

Very dense stands of *Ecklonia* occur on firm granite substrate. Undergrowth species are absent except for the presence of pink encrusting lithothamnia on the rock.

Both *Ecklonia* and the lithothamnia prefer well-agitated and sediment-free water and conditions are no doubt favourable where the swell passing around each side of the island causes intersecting wave patterns and a consequent continual water movement (Figure 4).

6. Osmundaria Prolifera Association

Common:—*Osmundaria prolifera.* Fairly common:—*Cystophora monilifera.*

Conditions:—Moderate surge.

Vertical Range:—3-8 m deep.

Although this association is relatively common in deeper sheltered waters of St. Vincent Gulf, it is poorly developed at West Island and occurs in only a few places in the more sheltered parts of Region B. The association has a simple structure and is dominated by *Osmundaria prolifera* with *Cystophora monilifera* as a characteristic associated species.

7. Red Algae Association

Common:—*Nizymenia australis, Rhodophyllis membranacea, R. multipartita, Plocamium angustum, P. mertensii, Rhodymenia australis, Ballia mariana.* Fairly common:—*Sonderophycus australis.* Occasional:—*Gelidium australe, Pterocladia lucida, Peyssonelia gunniana, Thamnoclonium dichotomum, Areschougia dumosa, Ballia callitricha, Haloplegma preissii, Hypoglossum protendens.* Rare:—*Cheilosporum elegans, Phacelocarpus labillardieri, Osmundaria prolifera.*

Conditions:—Reduced light and slight surge.

Vertical Distribution:—16-28 m deep on horizontal and sloping rock, occasionally shallower (see below).

This association is developed in the deeper, quieter waters about the island, i.e. in Region A and the outer part of Region B. The brown algae of the mid sublittoral gradually disappear between 10 and 15 m depth and are replaced by this community. However, *Ecklonia* may persist sporadically down to 24 m or more (Figures 7, 8, 14).

In shaded aspects and in calmer microhabitats such as depressions in the rock, the association occurs at levels up to 10 m but is best developed between 15 and 20 m deep. The association is floristically rich with 48 species recorded; plant cover is almost 100% with a two-layered structure. Some algae are commonly up to 30 cm high and there is in places a low ground layer of prostrate species—*Sonderophycus australis, Peyssonelia gunniana* and *P. novae-hollandiae*.

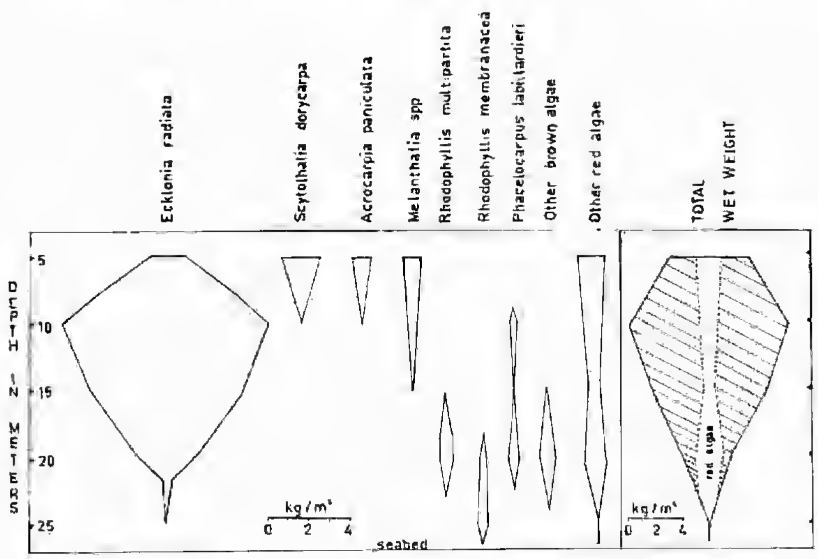


Fig. 9 Vertical distribution of wet weight of algae on horizontal surfaces between 5 and 27 m deep near Seal Rock in Region A (rough). The broken line indicates total weight of red algae.

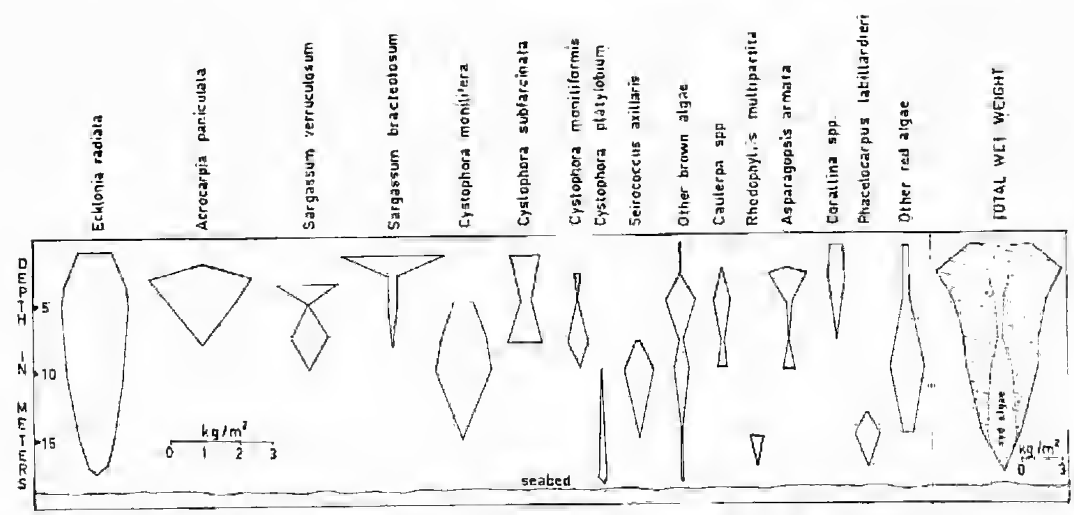


Fig. 10 Vertical distribution of wet weight of algae on horizontal surfaces between 2 and 18 m deep in Region B (moderately rough). The broken line indicates total weight of red algae.

Individual species of the upper layer may occur from single plants to patches up to 1 square meter in area. It is uncertain whether the observed patchiness is chance or is caused by ecological factors. Bergquist (1960a) comments on the same feature in New Zealand waters.

In deeper water (over 20-22 m), plant cover decreases to less than 10% as the fauna becomes dominant and covers the rock face. Frequently, algae in this region are attached to bryozoa. The number of species also declines and at 25 m only 15 species were recorded. At this depth red algae grow only on the upper faces of rocks, the steep faces of which are covered entirely by sponges, gorgonia, corals, bryozoa and hydroids. Some algal species become heavily epiphytised by bryozoans, hydroids and sponges. Changes in the composition of the association with depth are shown in Figures 8, 9 and 11.

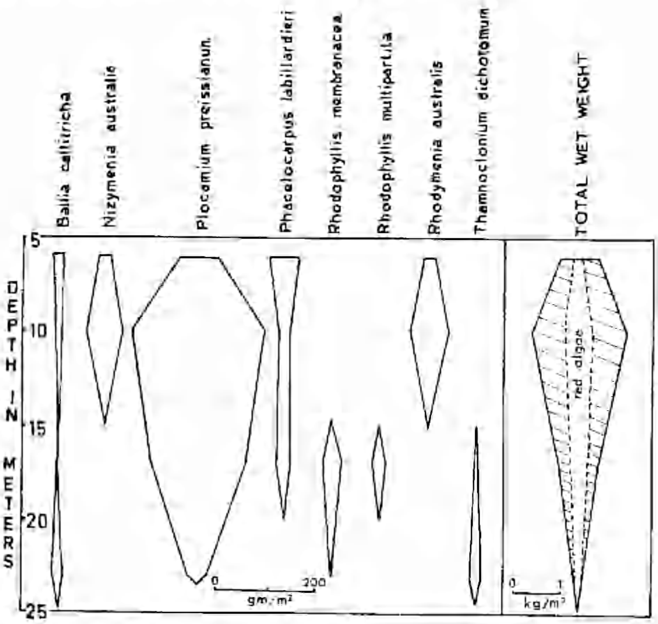


Fig. 11 Vertical distribution of wet weight of algae on vertical rock faces between 6 and 25 m deep at Seal Rock in Region A (rough). The shaded area represents total wet weight of *Ecklonia radiata*, which is not given as a separate diagram.

8. Caulerpa Communities

Several species of *Caulerpa* are of common occurrence about the island. As their fronds rise from creeping stolons often densely intertwined, communities which occur in favourable conditions spread over extensive areas. Except where surge is strong, particulate matter accumulates among the stolons and probably prevents establishment of other algae. These communities are well developed on upper surfaces of rocks in agitated shallow water with maximal light conditions and are not uncommon in similar habitats elsewhere on the southern Australian coast.

Caulerpa brownii community

Conditions:—Moderate surge.

Vertical Range:—Usually 1 to 1·5 m deep. Scattered plants as deep as 5 m.

The species forms a dense community of plants up to 10 cm in height, in Regions B and C, usually on upward facing rocks. Sometimes scattered plants of *Sargassum bracteolosum* and *Perithalia caudata* occur where the association is not dense. *C. brownii* is also common in the lower eulittoral algal mat in Regions B and C.

Caulerpa flexilis community

Conditions:—Moderate surge.

Vertical Range:—2-5 m deep.

The stolons form a dense basal mat sheltering a rich crustacean, molluscan and worm fauna. Above it the fronds form a dense cover to about 15 cm in height. At West Island the community prefers slightly deeper water than *Caulerpa brownii* and is found in Regions B, C and D.

Caulerpa obscura community

Conditions:—Moderate surge.

Vertical Range:—5-7 m deep.

This community is common on horizontal or sloping rocks in Region B in rather deeper water than either of the other Caulerpa communities. The fronds are up to 20 cm long and are a haven for very large numbers of amphipods and isopods.

SEASONAL AND OTHER CHANGES

Nearly all the prominent algal species (see Appendix) are present throughout the year, though some show pronounced seasonal growth. However data on many of the smaller species are not adequate to judge whether some might be strictly seasonal in occurrence. Many red algae also appear to live for up to two years and show at least two age groups; younger plants are relatively free from epiphytes such as hydroids and certain bryozoans whereas older plants are often heavily epiphytised.

Algal growth is vigorous from winter until early summer. By midsummer the vegetation has an impoverished appearance as many species shed their fertile parts. The following changes are conspicuous; *Scytothalia dorycarpa* and *Seirococcus axillaris* lose some fronds and receptacles; *Cystophora moniliformis* loses its ramuli, leaving only the bare primary and secondary axes; the fronds of *Caulerpa flexilis* and *C. brownii* disappear leaving only their stolons on the rock face; the corallines lose fronds and ramuli often leaving bare stalks. During March, strong growth commences and the vegetation soon regains its winter appearance. As previously described, *Sargassum bracteolosum* grows seasonally during spring and sheds its fertile fronds by late summer (February). The growth of *Ecklonia* appears to cease during mid-summer and at this time the plants often lose part of their thalli while the remainder is often grazed by the gastropod *Subninella undulata* (Solander).

After completion of the main part of this study some changes in the vegetation were noticed during the summer of 1969-70. The density of *Ecklonia* greatly increased on the boulder slope in Region D, where it had previously been sparse, and at a depth of 4 to 5 m *Cystophora monilifera*, which previously had occurred as scattered plants, formed dense stands over one metre in height. The understorey species of smaller brown algae largely disappeared from this canopied area and were replaced by a low mat of *Corallina cuvieri* and *Corallina* sp. The brown alga *Cladostephus verticillatus* was noticed for the first time and became abundant in places. The winter of 1969 was free of storms and these changes are probably attributable to the calm conditions which had prevailed since the winter of 1968.

Changes such as these will be followed over the next few years in order to judge the stability of the associations described in this paper.

ESTIMATES OF STANDING CROP

In order to assess the individual contribution of species to the total biota, a quantitative study was made at selected localities on both horizontal and vertical faces. Over 100 samples were collected between August and December in 1967 and in 1968 by using a hoop of area 1/6 m^2 on horizontal surfaces and 1/10 m^2 on vertical faces. The hoop was placed on a rock and the algae were scraped from within the area into a net and later examined and weighed. Because of the physical difficulty in obtaining samples in strong surge where 10 minutes might be occupied for each, random sampling techniques were not feasible and the following procedure was adopted. A visual assessment was first made of the locality to select a rock face on which the algae were considered to be representative of the average density and cover for that locality. Any rock face which appeared to be either unusually protected or subjected to extreme water movement was therefore avoided. A number of contiguous samples was then scraped from the rock over a horizontal distance of several metres. This was repeated at various depths and localities. On vertical cliff faces a site facing the direction of the swell was selected in each case to minimise local effects.

At any single locality, 5 or 6 samples were considered sufficient to adequately sample the fairly uniform red algal growth (although often more were taken), but for the patchily occurring larger brown algae a more extensive area was sampled and a proportion of the plants collected. The method used by Crossett and Larkum (1966) is very similar. The results are given in Figures 9-14. At Seal Rock and at Toad Head samples were taken at approximately 3 metre intervals vertically, and in Judith Cove at one metre intervals.

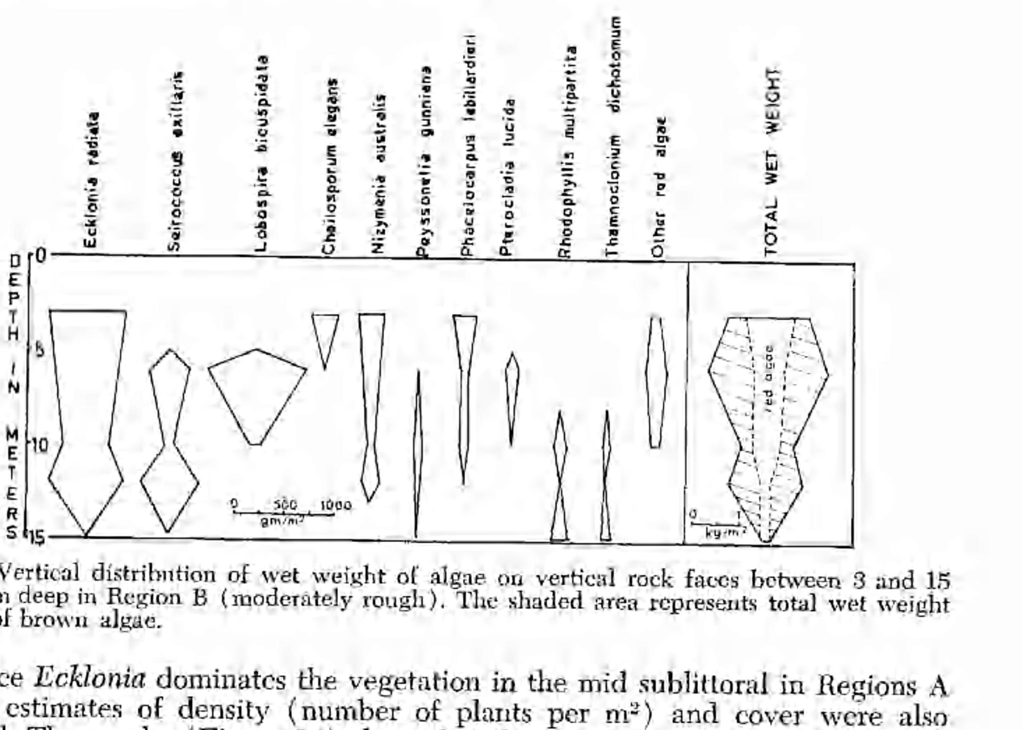


Fig. 12 Vertical distribution of wet weight of algae on vertical rock faces between 3 and 15 m deep in Region B (moderately rough). The shaded area represents total wet weight of brown algae.

Since *Ecklonia* dominates the vegetation in the mid sublittoral in Regions A and D, estimates of density (number of plants per m^2) and cover were also obtained. The results (Figure 14) show that the population density of *Ecklonia* is greatest (20+ plants per m^2) at a depth of 6 m in rough conditions (Region

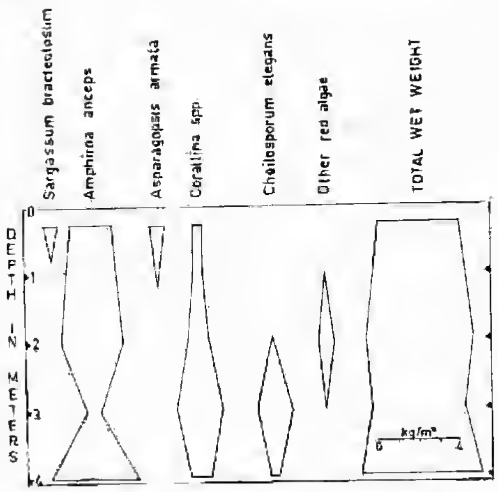


Fig. 13 Vertical distribution of wet weight of algae in *Amphiroa-Corallina* association in Region C.

A) and at 2-4 m depth in Region D. In Region B the highest density values are at a depth of 4-5 m but are much lower (5 plants per m²), probably due to competition from other species.

However, Figure 9 shows that the highest standing crop values (fresh weight) in Region A for *Ecklonia* occur at a depth of 10m, i.e., somewhat deeper than the depth at which the highest density values occur. This is because the size and weight of individual plants in very rough conditions (i.e. Region A, 5-8 m) is much less than in conditions where surge is moderate (the figures for mean plant weight being 95 g for the former conditions as compared to 600-800 g for less rough waters according to locality). Plants constantly subject to severe surge rarely develop to the size of those under less extreme conditions, and stipes with tattered or missing thalli are commonly seen after stormy weather.

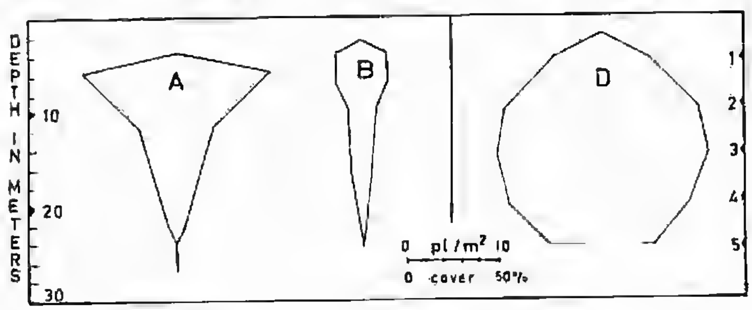


Fig. 14 Vertical distribution of plant density (as number of plants per square metre) of *Ecklonia radiata* on horizontal surfaces in Regions A, B and D.

DISCUSSION

The decrease in surge from rough to sheltered shores of the island is accompanied by conspicuous differences in the composition of the vegetation. The distribution of each species depends upon its particular response to and tolerance of various environmental factors. The survey has shown that groups of species have similar distribution patterns resulting in the occurrence of plant communities which persist throughout an area so long as the environment remains substantially unchanged. The same communities are seen in other places where a similar environment recurs. At several points abrupt changes in the type of community are also accompanied by a relatively steep gradient in surge or illumination, these being probably the two most important environmental factors.

TABLE 4

Showing the total number of species found in the various regions.

U.S.L. — Upper Sublittoral; M.S.L. — Mid Sublittoral. L.S.L. — Lower Sublittoral.

	Green Algae				Brown Algae				Red Algae				
	U.S.L.	M.S.L.	L.S.L.	Total	U.S.L.	M.S.L.	L.S.L.	Total	U.S.L.	M.S.L.	L.S.L.	Total	Total of all Species
Rough Region A	1	—	1	2	3	6	3	9	6	25	48	65	76
Moderately Rough Region B	2	7	—	7	3	24	—	24	2	60	—	61	92
Moderately Rough Region C	1	5	—	5	2	12	—	12	5	10	—	12	29
Semi-Sheltered Region D	1	5	—	5	1	16	—	16	4	5	—	6	27
Total Number of Species				9				30				93	132

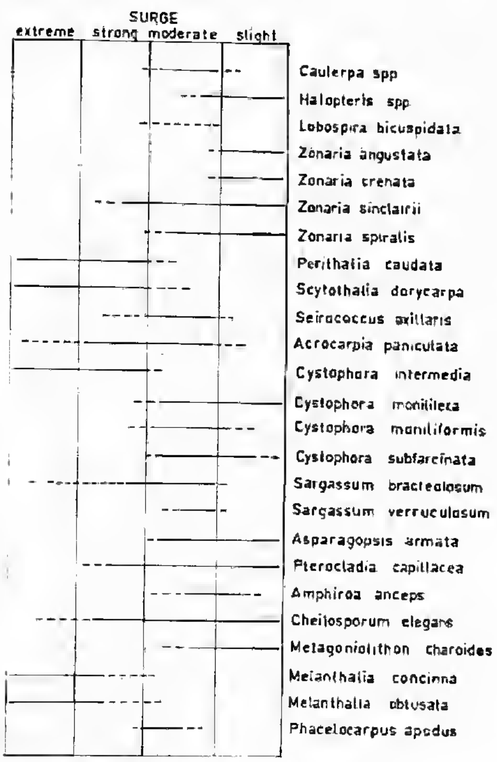


Fig. 15 Horizontal range of common algae of the mid-sublittoral. Extreme to strong surge —Region A. Moderate surge—Regions B and C. Slight surge—Region D.

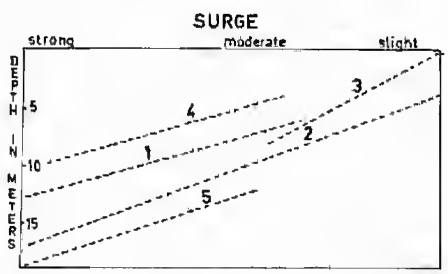


Fig. 16 Elevation of the upper limits for some species with reduction in surge.

1. *Lobospira bicuspidata, Seirococcus axillaris, Nizymenia australis, Rhodophyllis multipartita, R. membranacea.*
2. *Mychodea hamata, Osmundaria prolifera, Laurencia clavata.*
3. *Zonaria angustata, Zonaria spiralis, Asparagopsis armata.*
4. *Metamastophora flabellata, Cheilosporum elegans, Euptilota articulata.*
5. *Thamnoclonium dichotomum.*

A feature of the survey is that comparatively few species comprise the bulk of the vegetation while many species occur in small numbers or in a restricted locality.

Horizontal Distribution

The total number of species in the four regions varies considerably and their distribution in regions and zones is given in Table 4. It is apparent that a shore of moderate roughness favours the greatest number of species; this is due to the occurrence of two floristically rich communities viz. the Fucoid Association in the mid sublittoral and the lower sublittoral association of red algae. However, the latter association is better developed in the deeper waters of Region A where there is lower light intensity.

Figure 15 gives the horizontal ranges of some common species, mostly of the mid sublittoral, and it is evident that water movement is an important factor limiting the horizontal distribution of most algae to that part of the shore where suitable conditions exist. Some shade-tolerant species (see Figure 16) are able to extend their horizontal range by growing at a greater depth in rougher conditions.

Green algal (*Caulerpa*) communities require rather sheltered conditions and are distributed accordingly. Their occurrence at different depths probably reflects their particular requirements for light rather than for water movement.

Vertical Distribution

It must be re-emphasized here that this survey deals with the algae of horizontal and vertical or steeply sloping rock surfaces on a "steeply sloping" granitic island. These habitats are relatively uniform compared to those on calcareous coasts where rock platforms at about low tide level offer a great variety of pools and overhangs giving great diversity in microhabitat conditions of light and water movement. On such rock platforms (see Womersley 1948), many species recorded only from deeper zones (e.g. the mid sublittoral) on West Island are found in shaded or sheltered pool areas. At low tide, deep pools on rock platforms provide conditions of surge comparable to those at some depth.

Changes in algal vegetation with depth have been documented for many seas (for recent studies see Crossett and Larkum 1966, Jorde 1966, Kitching 1941, Neushul 1965, Petrov 1967, Vozzhinskaya 1965, and Zaneveld 1966). Other workers have shown experimentally that important controlling factors are gradients in light and water movement (see Conover 1968, Feldmann 1937, Jorde and Klavestad 1963, Levring 1947, 1966, 1968, Whitford and Kim 1966). These factors will now be discussed for each zone.

(1) *Upper Sublittoral Zone*

This zone, best developed in Region A, is dependent on rough conditions (Figure 6). Some species (*Curdiea gymnogongroides*, *Melanthalia* spp. and *Polyopes constrictus*) require high water movement and are restricted to this zone; others tolerate these conditions and range more widely in the sublittoral (e.g. *Gelidium glandulaefolium*, *Pterocladia capillacea* and *Corallina* spp). Strong light is a limiting factor for many species, but some brown algae (*Sargassum bracteolosum*, *Zonaria sinclairii*, *Cystophora subfarcinata* and *Acrocarpia paniculata*) and coralline algae (*Corallina* spp. and *Amphiroa anceps*) withstand full sunlight and even grow in momentarily emergent situations (see p. 118 and Figure 7). Feldmann (1951) attributes the success of corallines in high light intensities to the presence in their tissues of calcium carbonate which serves as a light shield. This probably explains their abundance in sunny aspects about the island.

In rough areas of West Island the upper limit of the upper sublittoral zone is marked by the sublittoral fringe zone of *Cystophora intermedia* (Womersley and Edmonds 1958, p. 233) as shown in Figure 7. This fringe zone is absent on less rough coasts (Regions B, C, D) where the mid sublittoral large brown algal associations approach closer to low tide level.

The lower limits of the upper sublittoral zone are often indicated by the tattered remnants of species characteristic of the zone below, suggesting that wave action prevents the encroachment of algae characterising the mid sublittoral by its destructive effect on these young plants, probably during storms, rather than by preventing their initial establishment.

(2) *Mid Sublittoral Zone*

The importance of surge rather than light in determining the depth at which an algal zone occurs is strikingly shown for the mid sublittoral zone. As shown in Figure 6, this zone is depressed in rougher conditions. In such cases surge conditions are of primary importance providing light intensities are still adequate for the species concerned.

The most conspicuous alga of this zone, *Ecklonia*, grows to a considerably greater depth in Region A (Figures 9, 10 and 14) than in the other regions, and in other rough ocean areas of South Australia occurs at much greater depths (Shepherd, unpublished data). Other West Island species whose lower limit is similarly extended by greater water movement are *Perithalia caudata*, *Gelidium australe*, *G. glandulaefolium*, *Pterocladia lucida*, *Cheilosporum elegans*, *Thamnoclonium dichotomum* and *Nizymenia australis*.

On the other hand some species of algae do not grow at greater depth in rougher conditions (e.g. *Acrocarpia paniculata*, *Cystophora moniliformis*, *C. monilifera* and *C. subfarcinata*) and it is probable that light attenuation is the critical factor determining the lower limit for these species.

Asparagopsis armata occurs principally as an epiphyte, but shows little preference for a particular algal host (see Appendix). It is unable to grow in very rough conditions but is prolific elsewhere. At its lower limits the species appears to be sensitive to reduced water movement. On European coasts the species has a narrower vertical range but its ecology is otherwise similar (see Dizerbo 1964).

A third factor which may be important in limiting the growth of some algae at depth is the nature of the surface film on the substrate. It has been observed that some algae (e.g. *Ecklonia*, *Scytothalia* and *Seirococcus*) only grow on clean rock surfaces. In deeper water, with reduced water movement, the rock is covered with sediments of various kinds. Such a surface may be unsuitable for establishment of these algae. This factor is clearly related to water movement and further studies are necessary to elucidate it.

(3) *Lower Sublittoral Zone*

This zone is occupied by species which are adapted to low light conditions and slight surge. The decrease in light below 25 m, associated with turbidity near the bottom, is probably responsible for the disappearance of algae just below this depth. However, other factors not investigated may also have some effect; these include the deposition of sediment previously mentioned (see Strachan and Koski 1969) and the smothering effect of epiphytic bryozoans on some algae. The lower limit for attached algae for the waters of Encounter Bay is probably about 30 m; further offshore, in deeper waters, the lower limit is known to exceed 35 m.

The factors determining the upper limit for red algae are problematic and it is not often possible to distinguish between the effects of light and surge.

Rhodophyllis multipartita and *R. membranacea* appear to be sensitive to both factors and are appreciably displaced upwards only with a combination of sheltered and shaded conditions (Figures 9-12). Some species appear to respond in the same way to reduced water movement (see Figure 16). However, it appears that most species of the mid and lower sublittoral are sensitive to strong light to some degree. Uplift of limits in shade has been noted for *Thamnoclonium dichotomum*, *Pterocladia lucida*, *Metamastophora flabellata*, *Ballia mariana* and *B. callitricha*. The last named species has a remarkable vertical range and is able to grow in deep shade in the upper sublittoral in rough conditions.

Standing Crop and Density

The variation in standing crop values taken on horizontal and vertical surfaces (Figures 9-12) further illustrates the effects of light and water movement on algae.

On vertical surfaces where light intensity is 10-40% of that on horizontal surfaces at a given depth (Table 3) there is a substantial reduction in the total weight of standing crop. This is due partly to changes in community structure and partly to competition for space with faunal elements which predominantly colonise steep or vertical surfaces.

Comparison of standing crop values in Region A with those of Region B (Figures 9-12) shows that, except at upper levels (0-8 m, Region A) where mechanical damage by wave action is considerable, there are higher standing crop values on both horizontal and vertical surfaces in the rougher locality. This is probably due both to the better conditions for growth provided by increased water movement and to associated effects permitting greater density of algae, such as the presence of a cleaner substrate and the depression of certain faunal species into deeper water.

In Region A the highest standing crop values for *Ecklonia* are 10·4 kg/m^2 (at 10 m) and there are even higher values of 16·8 kg/m^2 in Region D at 3 m depth. These values are comparable with values for *Laminaria hyperborea* forests on coasts about the North Sea (e.g. 11·1 kg/m^2 reported by Lüning 1969, and 6 kg/m^2, a mean of 59 surveys, found by Walker 1954).

Floristic Aspects

Further detailed collecting around West Island would doubtless considerably extend the total of 132 species of green, brown and red algae recorded in Table 4 (the commoner ones being listed in the Appendix). It is clear however that certain groups or genera are conspicuous in the sublittoral while others are notably absent.

In the Chlorophyta, only the genus *Caulerpa* is common (6 species and 3 recognised communities). In the Phaeophyta, the Dictyotales (especially species of *Zonaria*) and the Fucales are most conspicuous, though the only member of the Laminariales (*Ecklonia*) found on central South Australian coasts is ecologically important.

In the Rhodophyta, two genera of the Gigartinales are strikingly common, both in species and occurrence; these are *Plocamium* with 8 species and *Rhodophyllis* with four species. The Ceramiales are not widely represented compared to the large number of genera and species found in southern Australia; this applies especially to the family Rhodomelaceae. However, further collecting may well result in many additions of small species in this order.

With the exception of the coralline algae (which reach the lower eulittoral) and some of the large brown algae which reach to low tide level, all the species recorded (see Appendix) are found only in the sublittoral. The general lack of algae above low tide level on South Australian coasts has been documented by Womersley and Edmonds (1958).

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APPENDIX. ALGAL SPECIES LIST

The following list includes the commoner species collected during the survey but not those found only rarely. Further collecting, especially in other micro-habitats than vertical and horizontal rock, would doubtless increase the number of species. Womersley 1956b and 1967 give references to the southern Australian species of Chlorophyta and Phaeophyta respectively, but no single reference to the species of Rhodophyta is currently available. Specimens representative of all species are deposited in the Algal Herbarium, Department of Botany, University of Adelaide.

The distribution of each species is given as in the four regions recognised (A, B, C, D), followed by the depth range in metres. References to text figures concerning the species are given where appropriate.

Most species are present throughout the year, although some show their best development in spring and summer.

CHLOROPHYTA

ULVALES

Ulva lactuca L. B, 0-1; C, 0-1; D, 0-1.

CAULERPALES

Caulerpa brownii (C. Ag.) Endl. A, 0-3; B, 0-2; C, 0-2; D, 0-2. (Fig. 15).
Caulerpa cactoides (Turner) C. Ag. B, 5.
Caulerpa flexilis Lamx. B, 2-5; C, 2-5; D, 3. (Fig. 15).
Caulerpa geminata Harvey. A, 5; B, 8; D, 1. (uncommon).
Caulerpa obscura Sonder. C, 3-7; D, 4-5. (Fig. 15).
Caulerpa scalpelliformis (R. Br.) C. Ag. D, 4. (uncommon).

CODIALES

Codium pomoides J. Ag. A, 10-15; D, 5-7. (uncommon).

PHAEOPHYTA

SPHACELARIALES—Stypocaulaceae.

Halopteris funicularis (Mont.) Sauv. B, 3-6; D, 1-5. (Fig. 15).
Halopteris gracilescens (J. Ag.) Womersley. B. 3-6; C, 3-6; D, 1-5. (Fig. 15).
Halopteris pseudospicata Sauv. D, 3-5. (Fig. 15).

Cladostephaceae

Cladostephus verticillatus (Lightf.) C. Ag. D, 3-4.

DICTYOTALES—Dictyoteae.

Dictyota diemensis Kuetzing (narrow form). C, 1-5; D, 3-5.
Dictyota prolifera Lamx. B, 15-22.
Dilophus robustus (J. Ag.) Womersley. A, 10-13; B, 16. (Fig. 8).
Glossophora nigricans (J. Ag.) Womersley. A, 16-18; B, 10-22. (Fig. 8).
Lobospira bicuspidata Aresch. A, 13-25; B, 6-25; D, 2-6. (Figs. 8, 12, 15, 16). (commonly epiphytic on *Acrocarpia paniculata*, *Seirococcus axillaris* and *Phacelocarpus labillardieri*).
Pachydictyon paniculatum (J. Ag.) J. Ag. B, 3-6; D, 3-5.

Zonarieae

Dictyopteris muelleri (Sonder) Reinbold. A, 13-25; B, 16-26. (Fig. 8).
Zonaria angustata (Kuetz.) Pap. B, 13-22; D, 1-5. (Figs. 15, 16).
Zonaria crenata J. Ag. A, 22; D, 3-5. (Fig. 15).
Zonaria sinclairii H. & H. A, 0-5; B, 0-13; C, 0-5; D, 0-5. (Figs. 8, 15).
Zonaria spiralis (J. Ag.) Pap. A, 1-3; B, 10; D, 1-5. (Figs. 15, 16).

SPOROCHNALES

Carpomitra costata (Stackh.) Batters. A, 7-25; B, 13-22. (Fig. 8).
Perithalia caudata (Lab.) Womersley. A, 2-14; B, 5-10; C, 2-3. (Figs. 8, 15).

LAMINARIALES

Ecklonia radiata (C. Ag.) J. Ag. A, 4-22; B, 2-20; C, 1-5; D, 0-5. (Figs. 7-12, 14).

FUCALES—Seirococcaceae

Scytothalia dorycarpa (Turn.) Grev. A, 2-17; B, 10. (Figs. 7-9, 15).
Seirococcus axillaris (R. Br.) Grev. A, 14-20; B, 7-25; C, 4-5. (Figs. 8, 10, 12, 15, 16).

Cystoseiraceae

Acrocarpia paniculata (Turn.) Aresch. A, 3-11; B, 3-15; C, 3-5; D, 3-5. (Figs. 8, 9, 10, 15).
Cystophora intermedia J. Ag. A, sublittoral fringe. (Figs. 7, 15).
Cystophora monilifera J. Ag. B, 5-8; D, 1-5. (Figs. 10, 15).
Cystophora moniliformis (Esper) Wom. and Nizam. B, 1-9; C, 3-5; D, 1. (Figs. 10, 15).
Cystophora platylobium (Mert.) J. Ag. B, 10-18. (Fig. 10).
Cystophora subfarcinata (Mert.) J. Ag. B, 2-6; C, 3-5; D, 3-5. (Figs. 10, 15).

Sargassaceae

Sargassum bracteolosum J. Ag. A, 3-13; B, 0-10; C, 0-5; D, 0-2. (Figs. 10, 13, 15).
Sargassum verruculosum (Mert.) C. Ag. B, 4-16; D, 2-3. (Figs. 10, 15).

RHODOPHYTA

NEMALIONALES—Helminthocladiaceae

Liagora harveyiana Zeh. B, 3-6 (uncommon).

Bonnemaisoniaceae

Asparagopsis armata Harvey. A, 16-25; B, 6-16; C, 3-5; D, 0-2. (Figs. 10, 13, 15, 16).
(A common epiphyte on *Zonaria* spp., *Acrocarpia paniculata*, *Cystophora monilifera*, *C. moniliformis*, *Sargassum verruculosum*, *Gelidium glandulaefolium*, *Pterocladia capillacea* and *Amphiroa anceps*).

Delisea elegans (C. Ag.) Mont. A, 16-19; B, 13-16.
Delisea hypneoides Harvey B, 13 (uncommon).
Delisea pulchra (Grev.) Mont. A, 19-22 (uncommon).
Leptophyllis conferta (R. Br.) J. Ag. B, 13-22.

GELIDIALES

Gelidium australe J. Ag. A, 3-23; B, 3-13. (Fig. 8).
Gelidium glandulaefolium H. & H. A, 4-20; B, 6-10. (Figs. 7, 8).
Pterocladia capillacea (Gmel.) Born. & Thur. B, 3-6; C, 0-5; D, 0-5. (Fig. 15).
Pterocladia lucida (R. Br.) J. Ag. A, 4-22; B, 6-10 (Figs. 8, 12).

CRYPTONEMIALES—Squamariaceae

Peyssonelia gunniana J. Ag. A, 11-24; B, 13-22. (Figs. 8, 12).
Peyssonelia novae-hollandiae (Kuetz.) Harvey. A, 12-22; B, 12-18.
Sonderophycus australis (Sonder) Denizot. A, 8-26; B, 13-22. (Fig. 8).

Corallinaceae

Amphiroa anceps (Lamarck) Dcne. C, 2-5. (Figs. 13, 15).
Cheilosporum elegans (H. & H.) Aresch. A, 8-23; B, 3-16; C, 1-3; D, 3-5. (Figs. 8, 12, 13, 15, 16).
Corallina cuvieri Lamx. A, 0-2; B, 3-10; C, 2-5; D, 1-5. (Figs. 7, 10, 13).
Corallina sp. A, 0-3; B, 1-3; C, 1-5; D, 2-5. (Figs. 7, 10, 13).
The species of *Corallina* need detailed study; two taxa may be present under *C. cuvieri* and the status of *Corallina* sp., possibly related to *C. officinalis*, needs clarification.
Metagoniolithon charoides (Lamx.) W.v.Bosse. B, 2-6; D, 5. (Fig. 15).
Metamastophora flabellata (Sonder) Setchell. A, 10-18; B, 7-13. (Fig. 16).

Cryptonemiaceae

Carpopeltis phyllophora (H. & H.) Schmitz. A, 10-18; B, 6-13.
Epiphloea bullosa (Harv.) Schmitz? A, 10-16.
Polyopes constrictus (Turn.) J. Ag. A, 2-6; D, 0-2.
Thamnoclonium dichotomum (J. Ag.) J. Ag. A, 13-26; B, 10-13. (Figs. 8, 11, 12, 16).

GIGARTINALES—Gracilariaceae

Curdiea gymnogongroides J. Ag. A, 1-8; C, 2-3. (Figs. 7, 8).
Melanthalia concinna J. Ag. A, 3-10; B, 3-12. (Figs. 7, 8, 9, 15).
Melanthalia obtusata (Lab.) J. Ag. A, 6-16; B, 6-10; C, 1-2. (Figs. 7, 8, 9, 15).
var. *intermedia* (Harv.) J. Ag. A, 16-18; B, 6-10.

Plocamiaceae

Plocamium angustum (J. Ag.) H. & H. A, 3-28; B, 2-22. (Fig. 8).
Plocamium coccineum (Huds.) Lyngbye. A, 14-26; B, 10-15; D, 2. (Fig. 8).
Plocamium costatum (C. Ag.) H. & H. A, 15-20; B, 6-10. (Fig. 8).
Plocamium dilatatum J. Ag. A, 15-20; B, 10-16. (Fig. 8).
Plocamium leptophyllum Kuetzing. A, 20-24; B, 16-20.
Plocamium mertensii (Grev.) Harvey. A, 10-25; B, 6-16. (Fig. 8).
Plocamium patagiatum J. Ag. A, 10-25. (Fig. 8).
Plocamium preissianum Sonder. A, 3-17; B, 10-20 (Fig. 8).

Phacelocarpaceae

Phacelocarpus apodus J. Ag. C, 2-5. (Fig. 15).
Phacelocarpus labillardieri (Mert.) J. Ag. A, 5-26; B, 6-15. (Figs. 8-12).
Nizymenia australis Sonder. A, 13-25; B, 6-16. (Figs. 8, 11, 12, 16).

Solieriaceae

Callophycus laxus (Sonder) Silva. A, 10-20. (Fig. 8).

Rhabdoniaceae

Areschougia dumosa Harvey. A, 16-24; B, 13-16. (Fig. 8).
Areschougia laurencia (H. & H.) Harvey. B, 6-10.

Rhodophyllidaceae

Rhodophyllis marginalis J. Ag. B, 13-18.
Rhodophyllis membranacea (H. & H.) Harvey. A, 13-26; B, 10-23. (Figs. 8, 9, 11, 16).
Rhodophyllis multipartita Harvey. A, 10-26; B, 6-23. (Figs. 8-12, 16).
Rhodophyllis ramentacea (C. Ag.) J. Ag. A, 13; B, 13-18.

Hypneaceae

Hypnea episcopalis H. & H. A, 16-18; B, 6-16.

Mychodeaceae

Mychodea hamata Harvey. A, 15-18; B, 6-8. (Fig. 16).
Ectoclinium latifrons J. Ag. A, 13-17.

Acrotylaceae

Acrotylus australis J. Ag. B, 6-13.
Peltasta australis J. Ag. A, 10-16; B, 13-16.

RHODYMENIALES—Rhodymeniaceae

Rhodymenia australis Sonder. A, 13-26; B, 13-23. (Figs. 8, 11).

Champiaceae

Champia tasmanica Harvey. A, 16-22.

CERAMIALES—Ceramiaceae—Crouanieae

Gattya pinnella Harvey. B, 16-21.

Antithamnieae

Acrothamnion preissii (Sonder) Woll. A, 16; B, 6-13. (Epiphytic on *Gelidium australe*, *Pterocladia lucida*, *Nizymenia australis* and *Ballia callitricha*).
Ballia callitricha (C. Ag.) Kuetz. A, 5-25; B, 5-23. (Figs. 8, 11).
Ballia mariana Harvey. A, 10-26; B, 13-26. (Fig. 8).

Spongoclonieae

Haloplegma preissii Sonder. B, 16-26.
Spongoclonium sp. A, 13-20; B, 13-26.

Other species of *Spongoclonium* occur at Toad Head and Oedipus Point in 16-26 m. The species of this genus are confused and await monographic study.

Griffithsieae

Neomonospora elongata (Harvey) Womersley. A, 19-26; B, 13.
Neomonospora griffithsioides (Sonder) Womersley. B, 6-23.

Spyrideae

Spyridia opposita Harvey. A, 15-20; B, 10-13.

Ptiloteae

Euptilota articulata (J. Ag.) Schmitz. A, 10-20; B, 6-23. (Figs. 8, 16).

Delesseriaceae-Hypoglossum group

Hypoglossum protendens J. Ag. A, 16-26; B, 13. (Fig. 8).

Hemineura group

Hemineura frondosa (H. & H.) Harvey. A, 16; B, 19-26.

Phycodrys group

Crassilingua marginifera (J. Ag.) Pap. A, 10-19; B, 13-16.
Halicnide similans J. Ag. A, 16-26; B, 16-22.

Cryptopleura group

Acrosorium uncinatum (J. Ag.) Kylin. B, 19. Common as small plants on other algae in various depths of A and B.
Hymenena multipartita (H. & H.) Kylin A, 13-26.

Dasyaceae

Dasya ceramioides Harvey. B, 16-26.
Heterosiphonia australis (J. Ag.) De Toni. A, 21-26.

Rhodomelaceae—Polysiphonieae

Polysiphonia nigrita Sonder. B, 3-10. Epiphytic on *Acrocarpia, Scytothalia* and *Cystophora subfarcinata*.

Amansieae

Osmundaria prolifera Lamx. A, 18; B, 5-22. (Fig. 16).

Laurencieae

Laurencia clavata Sonder? A, 13-26; B, 6-23. (Fig. 16).
Laurencia elata (C. Ag.) Harvey. A, 6-10; B, 13; C, 1-2.
Laurencia filiformis (C. Ag.) Mont. B, 6-23.

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EXPLANATION OF PLATE

PLATE 1

Fig. 1. Aerial photograph of West Island showing Encounter Bay and Victor Harbor to the north east.

(photograph A. R. Milne)

Fig. 2. Aerial photograph of West Island showing the main localities.

(photograph A. R. Milne)